

**PARASITISM OF SWEAT BEES IN THE GENUS *AGAPOSTEMON*  
BY CUCKOO BEES IN THE GENUS *NOMADA*  
(HYMENOPTERA: HALICTIDAE, ANTHOPHORIDAE)**

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*Nomada* is a large Holarctic genus of cleptoparasitic ("cuckoo") bees whose species superficially resemble wasps. Most species parasitize soil-nesting bees in the genus *Andrena* (Andrenidae), but a few have been recorded from other soil-nesting Andrenidae (*Panurgus*, *Nomadopsis*), Halictidae (*Halictus*, *Lasioglossum*, *Evyllaesus*, *Nomia*), Melittidae (*Melitta*, *Dasyopoda*), and Anthophoridae (*Eucera*) (Stoeckhert, 1933, 1954; Stephen, Bohart, and Torchio, 1969; Bohart, 1970). Despite the abundance of many species of *Nomada*, only Linsley and MacSwain (1955) have conducted detailed studies of their biology. Rozen (1966) described the larvae of five species and he (Rozen, 1977) also described the pupa of one species and summarized nomadine behavior.

In this paper we record the first definite association between species of *Nomada* and host species in the sweat bee genus *Agapostemon* (Halictinae). Species of *Nomada* previously had been suspected of parasitizing species of *Agapostemon* (Linsley, MacSwain, and Smith, 1954; Roberts, 1969) but were never recovered from nest cells. We also present observations on nest-entering behavior, development of immature stages, and incidence of parasitism to supplement the meager biological data on *Nomada*.

#### Materials and Methods

*Nomada* (*Nomadula*) *articulata* Smith was studied in Ithaca, Tompkins Co., New York, principally on the Cornell University campus. J. A. made a detailed study of the above-ground behavior of one of its hosts, the univoltine, communally nesting *Agapostemon virescens* (Fabricius), at an aggregation of 13 nests in a 2 sq. m area in a weedy, sporadically mowed campus location in 1975 (Abrams, 1977<sup>1</sup>). Three female *N. articulata* were captured as they emerged from host nests, on 1 and 3 June and 5 July. She observed 15 female parasites at the nest site in June and July. Eleven of these were marked for individual recognition; seven reappeared at the nest site. She also recovered three adult *N. articulata* in host nests excavated in October. At the same site, G.C.E. excavated a nest containing immature *N. articulata* on 18 July 1972. G.C.E. also recovered *N. articulata* from nests of univoltine *Agapostemon radiatus* (Say) in a level, moist,

grassy lawn on the Cornell campus about 270 m from the nest site of *A. virescens*. Five nests, excavated on 19 July 1974, 23 June 1978, and 25 July 1978, contained immature *Nomada*. Adult *Nomada* were collected at the site but we did not conduct detailed behavioral observations.

*Nomada (Micronomada) formula* Viereck was studied near Richmond, Contra Costa Co., California, at the entrance to San Pablo Reservoir. G.C.E. observed *Nomada* flying about an aggregation of active nests of *Agapostemon texanus* Cresson located in level, bare, dry sandy soil, on 22 and 29 August 1975. He excavated five nests that contained immature *N. formula* on 24 and 25 September.

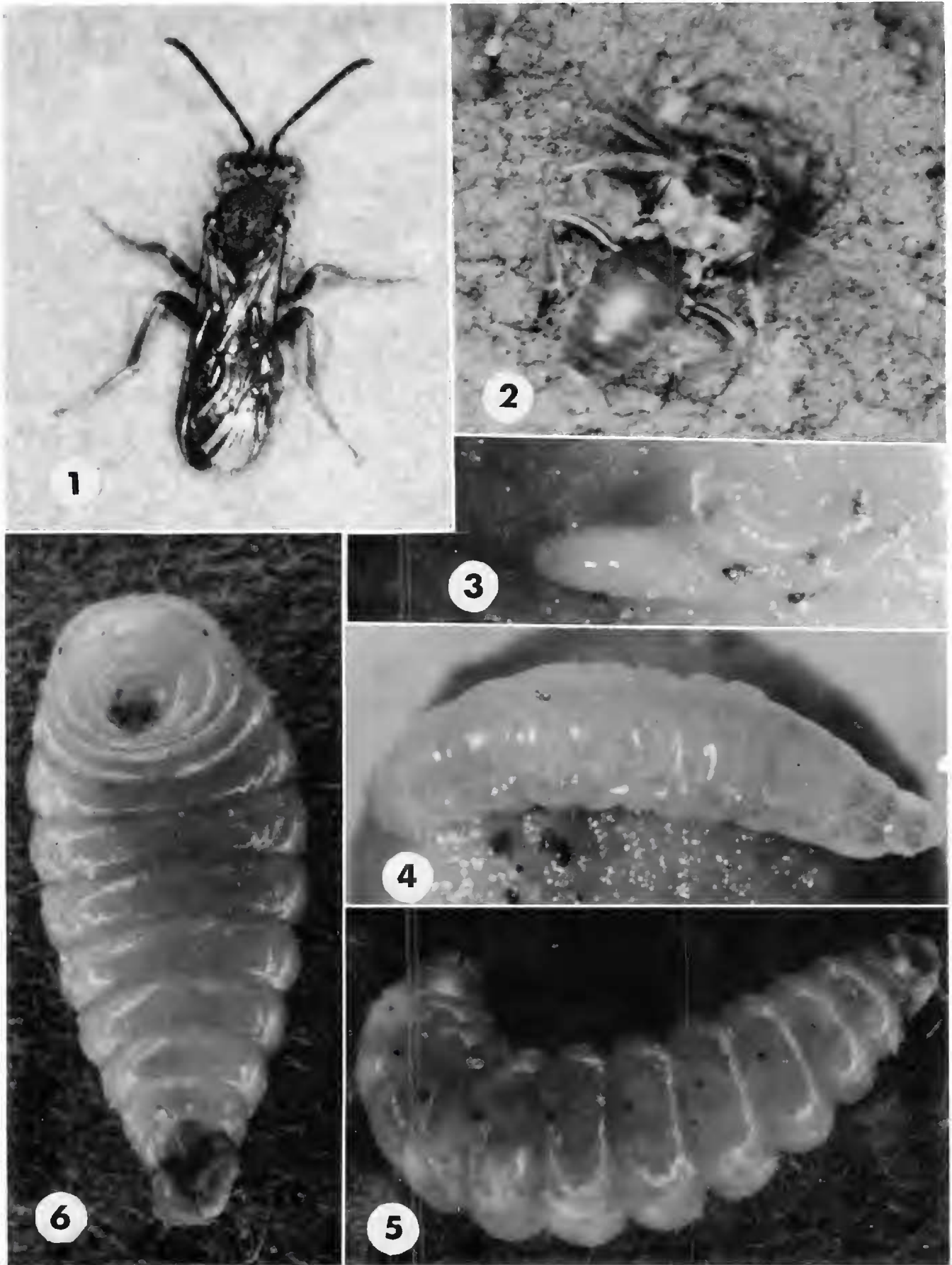
Techniques of observation, nest excavation, and rearing and preservation of immature bees are given by Abrams and Eickwort (1980a). In addition, some prepupae were kept in a refrigerator for several months to break diapause. Twenty-nine *N. articulata* immatures and 12 *N. formula* immatures were recovered from nest cells, of which six of the former and two of the latter species were reared to adults.

Voucher specimens of cleptoparasites and hosts and their immature stages are deposited in the Cornell University insect collection, lot number 995. Larvae and pupae of *Nomada* are also deposited in the American Museum of Natural History.

#### *Nomada (Nomadula) articulata* Smith

Marked adult females returned repeatedly to the *Agapostemon virescens* nest site. One female, marked on 2 July, visited the site on 15 of the next 18 observation days. Females were active from 0800 to 1230 hr. They flew in both sun and shade, but not when air temperatures were below 22°C. Typically a female visited the aggregation once or twice per morning and remained each time from 15 to 45 minutes, repeatedly attempting to enter nests. Her behavior was similar to that of *Nomada opacella* Timberlake and *Nomada* sp. at *Andrena* nest sites in California (Linsley and MacSwain, 1955; Thorp, 1969). *Nomada articulata* flew slowly through the aggregation a few centimeters above the ground and alighted on raised perches of earth, twigs, leaves, or stones, 3 to 12 cm from nest entrances. A female waited on the perch with her antennae directed towards the nest opening from 5 sec to 10 min before approaching the entrance (Fig. 1). About half of the attempts to enter nests were made immediately after an *Agapostemon* had left on a foraging trip. The other attempts were made just after an *Agapostemon* had entered her nest or when no activity could be seen at the nest entrance. *Nomada* did not approach a nest if a guard was visible at the entrance.

Each *N. articulata* female followed the same behavioral sequence when attempting to enter an *A. virescens* nest. She walked slowly towards the



Figs. 1-6. *Nomada articulata*. Fig. 1, adult female perched near host nest. Fig. 2, adult female attempting entry into nest of *Agapostemon virescens*. Fig. 3, first instar larva on egg of *A. virescens*. Fig. 4, larva feeding on provision mass of *A. virescens*. Fig. 5, prepupa, lateral view. Fig. 6, prepupa, ventral view.

nest entrance with her wings vibrating. She stopped at the entrance, still fanning her wings, and inserted her antennae into the burrow for 1 or 2 sec (Fig. 2). She then stopped vibrating her wings and walked into the burrow.

If the *Nomada* encountered an *Agapostemon* guard when she inserted her antennae into the nest entrance, she immediately backed away from the burrow and returned to a watching position or investigated another nest. The guard either snapped at the intruder with her mandibles or advanced towards the *Nomada* until her thorax was outside the entrance. If the guard was further down the burrow, the *Nomada* entered the nest but always reappeared within 10 sec. The guard followed the *Nomada* to the surface and blocked the nest entrance with her head or the dorsal surface of her abdomen. Of 50 attempts to enter nests, 48 were unsuccessful.

*Agapostemon virescens* did not interact with *Nomada* outside the nests. Guards did not chase parasites perched nearby, and on several occasions a returning forager flew right over a *Nomada* in order to enter her nest. In these instances, the *Nomada* immediately retreated.

Only one nest was entered successfully in 1975, by two *N. articulata* females on 1 July. This was the only nest in the aggregation that was occupied by a solitary *Agapostemon* female during the pollen-foraging season. July 1 was the only day that the host was seen foraging. She brought a load of pollen into her nest at 0936, emerged at 0941, and flew away. At 0957 an unmarked *N. articulata* entered the nest and remained in the burrow 3 min before emerging. The *Agapostemon* brought in two more pollen loads by 1050. At 1055, a second, marked *Nomada*, which had just been driven away from a communal nest, entered this nest and also remained 3 min before departing. Observations on 1 July were ended at 1100 hr. Although the nest entrance was open for the next three days, the *Agapostemon* had apparently abandoned her nest because she was never seen again. Two *Nomada* approached the nest entrance during these three days but neither descended into the burrow. Like other nomadines (Rozen, 1977), *N. articulata* probably oviposits only in host cells that are in the stage of being provisioned.

In two more instances in 1975, *Nomada* may have successfully entered nests of *A. virescens*. Both cleptoparasites were found trapped under plastic cups that were used to check exiting *Agapostemon*. Since *Nomada* walk to hosts' nest entrances, they may have approached the burrows through the gap between the ground and the edge of the cup. In one of these cases, a guard was blocking the nest entrance with the dorsal surface of her abdomen. The *Nomada* had apparently been stung, because she was partially paralyzed and died within 10 min.

*Nomada opacella* makes orientation flights after examining host burrows (Linsley and MacSwain, 1955). Most *N. articulata* had probably learned nest locations before we began constant observations at the Cornell nest

site, but one female was observed making an orientation flight. On 5 July, the female *Nomada* emerged from an *Agapostemon* nest at 0855 hr. She remained at the nest site, walking and taking short flights, until 1028 and then flew off. At 1121 she returned and attempted to enter a second nest, but was stopped by a guard. She then made a short orientation flight of three or four loops and left the nest site. On 6 July, she returned and attempted to enter both the nest from which she had first emerged and the second nest that she had located on 5 July.

In the nest of *A. virescens* excavated in 1972 that contained *Nomada* immatures, at least four of 13 cells (31%) were infested by the cleptoparasite. This nest also contained only one adult host. In contrast to *A. virescens*, *Agapostemon radiatus* made solitary nests that were scattered and well hidden in the grassy lawn. Five of the six excavated nests of *A. radiatus* yielded *Nomada* immatures, with percentages of infested cells for each nest of 100% of 8 cells, 93% of 14 cells, 50% of 2 cells, 33% of 6 cells, and 25% of 4 cells. The percentage of infested cells from all nests in this site was 63% of 40 cells; for infested nests only, 74% of 34 cells. Another nest of *A. radiatus*, well separated from nests of other *Agapostemon* in another lawn, yielded no *Nomada*.

We did not recover eggs of *N. articulata*, but they probably were placed in the cell walls, as occurs in all other Nomadinae (Rozen, 1977). *Nomada edwardsii* Cresson and *N. opacella* usually lay two eggs in each cell and the larva that first hatches kills the other egg (Linsley and MacSwain, 1955). The presumed oviposition period of *N. articulata* was half as long as the 4 to 6 min recorded for *N. opacella*, so double oviposition may not occur in *N. articulata*. We recovered first-instar *N. articulata* larvae on two provision masses. One larva apparently was in the act of consuming the host egg when we broke into its cell. The larva was situated parallel to and partially on top of the egg (Fig. 3). We brought the provision mass into the laboratory and provided another host egg. The mobile first-instar *Nomada* also killed this egg. All other *N. articulata* larvae were on provision masses without host eggs or larvae, so killing host eggs is typical of the first instar of this species, as it is of most Nomadinae (Rozen, 1977). Later instars (Fig. 4) perched on top of and consumed provision masses in the manner illustrated for other *Nomada* by Linsley and MacSwain (1955).

Mature *N. articulata* larvae from three nests defecated and then became quite turgid, resting on their dorsa in the cells with their elevated heads towards the cell mouths (Figs. 5–6), as illustrated for *N. suavis* Cresson by Bohart (1970). They presumably would have spent the winter as postdefecating larvae (prepupae), pupated in the spring, and emerged as adults along with their hosts in late May or early June. This developmental pattern is typical for Nomadinae (Rozen, 1977). In the laboratory, these prepupae

entered diapause and did not further develop unless they were refrigerated for several months. This cold treatment broke diapause, and development resumed when the bees were brought to room temperature.

However, *N. articulata* immatures from an *A. radiatus* nest excavated on 25 July 1978 did not follow this pattern. Ten were already pupae when the nest was excavated, and development of those that survived proceeded immediately to the adult stage without refrigeration. Three adult *N. articulata* were found in nests of *A. virescens* in October. Overwintering of adults was hypothesized for *Nomada* parasitizing vernal *Andrena* by Linsley and MacSwain (1955) and by Thorp (1969). Our data show that *N. articulata* from the same population and indeed the same nest site may overwinter both as prepupae and as adults.

#### *Nomada (Micronomada) formula* Viereck

*Agapostemon texanus* nests were aggregated, although each was believed to be occupied by a single female. The population was probably multivoltine, with provisioning for the last generation occurring in late August when adult *N. formula* were also present at the nest site. Flight activity of parent hosts and of cleptoparasites had ceased by late September, when nest burrows were partially filled with soil and no live parent females were in the nests. Most of the host cells were deserted at this time; a few contained older host pupae. Some newly emerged adult female hosts were in burrows or in hibernacula similar to those of *A. virescens* (Abrams and Eickwort, 1980a).

All *Nomada* recovered during these excavations were turgid postdefecating larvae. As with *N. articulata*, they were on their dorsa with their elevated heads towards the cell mouths. The feces appeared to be plastered on all the cell walls, although denser posteriorly. These feces often were separated from the cell walls and appeared to form a loose, amorphous, cocoon-like structure around the larva, the cylindrical fecal pellets being held together by silk-like strands (these may have been fungal mycelia). This loose configuration may have been due to the low soil moisture. Stephen, Bohart, and Torchio (1969) noted that *Nomada* larvae speckle cell walls with fecal pellets oriented in various directions.

No pupal or adult *N. formula* were recovered during the excavations, so that population was overwintering as diapausing prepupae. Several prepupae were refrigerated in the spring of 1976 and these moulted into pupae and then adults when removed to room temperature.

It was impossible to estimate parasitism rates in the largely deserted nests of *A. texanus*, although all five burrows traced to cell level appeared to lead to some cells that contained *Nomada* prepupae. Twelve *Nomada* prepupae

were recovered in total. In contrast, a large isolated nest of *A. texanus* located several hundred meters from the aggregation contained no *Nomada*.

### Discussion

The *Nomada* that attack *Agapostemon* behave very much like those that attack *Andrena*, despite the differences in host biology and phylogenetic relationship, and despite the fact that *Agapostemon* is a basically Neotropical genus whose species have been in contact with species of the Holarctic genus *Nomada* for presumably a relatively short period of evolutionary time. Indeed, *Andrena* nests were abundant in the nesting areas of *A. radiatus* and *A. virescens*, and quite possibly *N. articulata* is primarily an *Andrena* parasite that enters *Agapostemon* nests when it encounters them. Several European species of *Nomada* (i.e., *N. fucata* Panzer, *rufipes* Fabricius, and *zonata* Panzer, see Stoeckert, 1933) have been recorded as parasites of both halictines and *Andrena*.

Tengö and Bergström (1977) have analyzed the cephalic secretions of several species of *Nomada* and found an interesting pairwise correlation between the secretions of the male (but not the female) cleptoparasites and the Dufour's gland secretions of the females of their host species of *Andrena*. The male *Nomada* coats his mate with this secretion during copulation so she has the same odor as the host nest. Presumably the female is then able to enter a nest without being attacked by the host female. However, if some *Nomada* do indeed attack hosts belonging to more than one family, then either chemical mimicry does not occur in these species of *Nomada* or host species belonging to different genera produce similar chemicals in their Dufour's glands.

The behavior of *N. articulata* at nests of *A. virescens* and the heavy parasitism of some nests of *A. radiatus* and *A. texanus* by *Nomada* while others were untouched indicates that the *Nomada* learned the locations of nests and repeatedly returned to them. Such learning is apparently widespread in cleptoparasitic bees, as reviewed by Rozen, Eickwort, and Eickwort (1978). We hypothesize that *N. articulata* were "traplining," visiting each remembered nest in turn and, when a host female was not present, pausing long enough to check for cells being provisioned.

Solitary *Agapostemon radiatus* and *A. texanus* appear to be defenseless against such a strategy once their nests are discovered. Their only effective counter-strategies are to conceal their nest entrances more effectively and, especially, to build nests distant from those of other potential hosts. In contrast, communal *Agapostemon virescens* escape parasitism by *Nomada* through effective nest guarding, and only the occasional solitary nest of this species falls prey to the cleptoparasite (Abrams and Eickwort, 1980b).

A final point is the overwintering of *N. articulata* from the same population in two different stages, as prepupa and as adult. Similar developmental flexibility has been observed in several species of *Osmia* (Megachilidae) (Levin, 1966; Rust, 1974).

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### Footnotes

<sup>1</sup> *Nomada articulata* was erroneously identified as *Nomada australis* Mitchell in Abrams (1977).

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### NOTICE

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